SHORT COMMUNICATION

Male tawny dragons use throat patterns to recognize rivals

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Abstract The ability to distinguish between familiar and unfamiliar conspecifics is important for many animals, especially territorial species since it allows them to avoid unnecessary interactions with individuals that pose little threat. There are very few studies, however, that identify the proximate cues that facilitate such recognition in visual systems. Here, we show that in tawny dragons (*Ctenophorus decresii*), males can recognize familiar and unfamiliar conspecific males based on morphological features alone, without the aid of chemical or behavioural cues. We further show that it is the colour pattern of the throat patches (gular) that facilitates this recognition.

Introduction

An animal's ability to distinguish between familiar and unfamiliar conspecifics can be beneficial in many contexts, especially in the recognition of neighbours and intruders in territorial species (Tibbetts and Dale 2007). This ability allows residents to avoid the costs of fighting individuals that pose little threat (Temeles 1994; Fayed et al. 2008). Recognition of familiar conspecifics, such as neighbours, through chemical or auditory channels has been well

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documented (Vannoni and McElligott 2009), but, somewhat surprisingly, studies of visual signals have received far less attention (Parr et al. 2000; Whiting et al. 2009; Stuart-Fox et al. 2007). Studying visual signals requires teasing apart two types of signal-static (morphological) and dynamic (behavioural) (Osborne 2005a, b).

Most tests of vision-based recognition of familiar and unfamiliar conspecifics involve moving a neighbour and focal male to an unfamiliar setting, or replacing a neighbour with a stranger, and documenting the response of the focal male (Husak and Fox 2003; Osborne 2005a, b). While this method may demonstrate that lizards can differentiate between neighbours and strangers, it does not identify the specific signal/s that facilitates recognition or quantify the role of static and dynamic signals. There are surprisingly few studies that identify the exact visual signals that are used to differentiate between familiar and unfamiliar conspecifics: facial and abdominal markings in paper wasps (Tibbetts and Dale 2007), carapace colour patterns in fiddler crabs (Detto et al. 2006), colour patterns in threespot damselfish (Thresher 1979), and head bobbing in iguanas (Phillips 1995).

Studies usually document recognition by comparing the response of a focal male to a rival that he has previously encountered (familiar male) to his response when facing an unknown rival (unfamiliar male). This method is complicated by the fact that previous fighting experience is likely to affect the response of the focal male, and it is often the case that winners continue to win (Jackson 1991). If a male won his last fight, he might be more aggressive to a 'familiar loser' since he has greater certainty of winning the encounter; or he may be less aggressive since he is likely to win with minimal effort and cost. However, if a male lost his last fight, then the prediction is clear: he should be less aggressive towards the same male during the next encounter than to a male he has not previously fought. We suggest that it is, therefore, preferable to restrict the test comparison to the

difference in response by focal males to: (1) a male that they previously lost to in a fight and then (2) to a male that they have not previously fought. This way the focus is on losers rather than winners. If males can distinguish between familiar and unfamiliar rivals, then the prediction is that males should be less aggressive to rivals against whom they have previously lost than to rivals that they have not previously fought. If they are unable to recognise their rivals, they should show no difference in aggression to both types of males (all else being equal).

Here, we examine whether male tawny dragons (*C. decresii*) use visual cues to differentiate between rivals. Males are highly territorial and aggressive towards intruders (Osborne et al. 2012; Umbers et al. 2012) using elaborate, time-consuming, and conspicuous displays (Gibbons 1977; Stuart-Fox et al. 2003). Because a combination of morphological and behavioural signals elicit rival recognition (Osborne 2005a), here, we eliminate both behavioural and chemical cues to determine if morphology alone is sufficient for rival recognition. We then examine whether gular colour pattern is the cue used in recognition. It is a likely candidate since males have unique gular colour patterns (Stuart-Fox and Johnston 2005, Fig. 1) consisting of a single colour or a combination of yellow, blue or orange, either solid or in patterns of bars and dots (Stuart-Fox et al. 2004). Also, gular colour pattern is fixed through adulthood (Gibbons and Lillywhite 1981) and is exposed during aggressive encounters (Osborne personal observation). We conceal the colour patterns of stimulus males and note whether focal males are less aggressive towards a stimulus male that they had lost to in a fight than to a male that they had not previously encountered. We predict that males will be less aggressive to a rival with whom they had recently lost than to a previously unencountered rival. If gular colour pattern is essential for individual recognition, we predict that there would be no difference in the level of aggression towards familiar and unfamiliar males when these colours are obscured.

Methods

Adult males were collected from a wide area of the Flinders ranges in South Australia so that individuals had not previously interacted. They were housed individually in outdoor cages at The Australian National University (details in Osborne 2005a).

Methods for all interactions

Males were size-matched using a principal components analysis that incorporated mass, snout–vent length and head width. This is preferable to using a single size variable in lizards (Osborne 2005a). Thirty-two lizards were sorted into 16 size-matched pairs. Contests were conducted in a glass tank (150×50×50 cm). On day 1, an initial set of contests was run to create pairs of lizards that had fought each other. After acclimation, the divider was removed and pairs were allowed to interact until a winner and loser was identified. We identified the loser of the contest as the male that showed no assertive behaviour such as aggressive posturing, but rather lowered his crest and/or fled to his refuge when the winner postured or approached. Most contests were resolved without attempted physical fighting. All lizards recovered within 15 min with no signs of distress. The lizards were then left overnight with the opaque divider in place. Lizards that lost their first encounter were used as focal 'losers' in the subsequent, day 2, trials.

Experiment 1

On day 1 we placed pairs of lizards (one focal and one stimulus male) in the glass tank with a one-way mirror separating them so that the focal male could see the stimulus male but not the other way around. This avoided eliciting displays from the stimulus lizard as they seldom respond to mirror reflections (Gibbons and Lillywhite 1981). The non-

Fig. 1 Photos of some of the intra-population colour variation displayed in the gular region of adult male *C. decresii*. Photos by first author

moving stimulus lizards sat with their legs flat but the head raised up, sphinx-like, exposing their gular colour pattern to their rival (the focal male). Furthermore, we eliminated any trials in which the stimulus lizard moved during the trial to avoid the confounding effect of the stimulus lizard's behaviour on the response of the focal male. The partition also eliminated chemical cues because *Ctenophorus* dragons deposit on and detect chemical cues from surfaces by tongue flicking, rather than in the air (Jansson et al. 2005).

On day 2, each focal male ('losers' from day 1's trials) was presented sequentially with two stimulus lizards (order randomised): an unfamiliar lizard and a familiar lizard (the stimulus lizard that had beaten him the previous day). The behaviour of the focal lizard was filmed for 15 min using a Panasonic NV-DS28 digital video camera. There was a 2-h rest period between presenting the two stimulus lizards. All contests were carried out between 10 am and 1 pm, when the animals are naturally active. To verify the repeatability of our results, the entire experiment was repeated after a 2-week period from the last encounter in the trial, with no combination of two males ever used twice (focal lizards were presented with new familiar winner males and unfamiliar males in the repeat experiment). We analysed the two sets of experiments separately and present both sets of statistics.

We documented the behaviour of the focal lizard using a weighted index that is a conservative measure of male aggression commonly used in lizard studies (Osborne 2005a; Stuart-Fox and Johnston 2005). It is calculated by adding the scores for each behaviour during a single encounter with a stimulus lizard. The scores were: hind-leg push-up display=3 points; attempted approach=2 points; aggressive posturing=2 points; fleeing=-2 points; tail flick=-2 points (see Osborne 2005a for details). Each focal male was assigned an aggression index for each encounter with a stimulus male. Higher scores represent more aggressive behaviours. We compared the aggression scores for focal male encounters with unfamiliar versus familiar rivals that had previously beaten them using a Wilcoxon signed-ranks test.

Experiment 2

We ran a second experiment using the same experimental design as above, but with the additional step of obscuring the gular colour pattern on all stimulus lizards. We concealed the gular colour patterns with blue cream eye shadow (similar to the dorsal colour of these lizards). We again compared the focal male's aggressiveness towards an unfamiliar and familiar stimulus male and ran the entire experiment twice with new familiar winner males and unfamiliar males in the repeat experiment.

Results

Experiment 1

Focal males were more aggressive toward unfamiliar rivals than familiar rivals (against whom they had lost a fight the previous day) (Fig. 2). In the first set of trials, the mean aggression score was 5.2 ± 2.3 towards an unfamiliar male and -4.0 ± 1.2 towards a familiar male (Wilcoxon, $Z=3.301$, $P=0.001$, $N=16$). In the second (repeated) set of trials the mean aggressive score with 4.8 ± 3.0 towards an unfamiliar male and -2.4 ± 0.4 towards a familiar male (Wilcoxon, $Z=3.306$, $P=0.001$, $N=14$)

Experiment 2

When the gular colour patterns were obscured, focal males showed no difference in aggression towards familiar and unfamiliar stimulus males (Fig. 2). In the first set of trials, the mean aggression score was 4.2 ± 2.0 towards unfamiliar lizards and 8.7 ± 2.3 towards familiar lizards (Wilcoxon, $Z=1.82$, $P=0.07$, $N=20$). In the second (repeated) set of trials, the mean aggressive score was 2.9 ± 1.4 towards unfamiliar lizards and 4.2 ± 2.3 towards familiar lizards (Wilcoxon, $Z=0.31$, $P=0.76$, $N=17$).
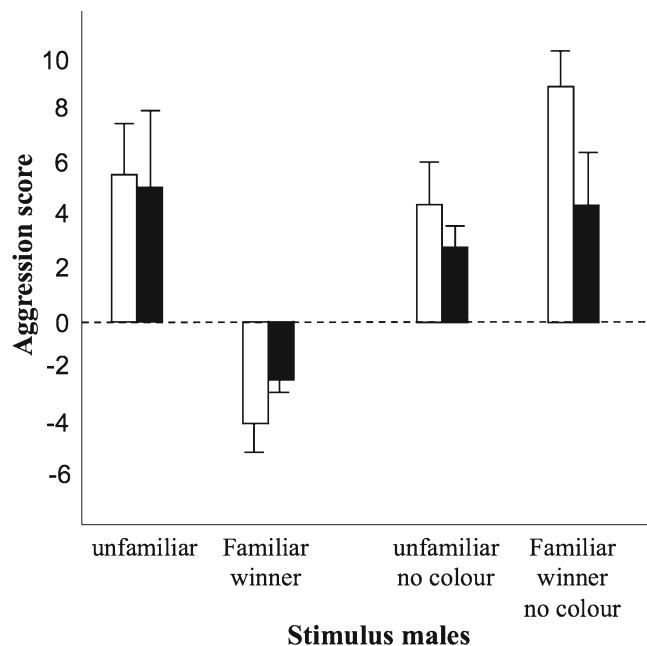
Fig. 2 Aggression scores for the four categories of stimulus males (mean with s.e. bars). *Clear bars* represent the initial trials and *dark bars* the repeated trials

Discussion

Males were more aggressive towards lizards that they had not previously fought than to those against whom they had recently lost. This suggests that they can identify familiar rivals and thereby avoid the costs associated with fighting superior competitors (Osborne 2005a). What signal facilitates this recognition? Only morphological signals were available to the males since both chemical and behavioural signals were eliminated. Of the available signals, the gular colour pattern is the most likely candidate for use in recognition. When we obscured the gular colour pattern of the stimulus lizards, focal males showed no measurable difference in aggression towards unfamiliar males and familiar males against which they had recently lost a fight. This suggests that focal males were no longer able to differentiate between potential rivals, providing evidence that the gular colour pattern is an essential cue for rival recognition in C. decresii. It is also possible that our method of concealing gular patterns made the rivals look abnormal and thus lizards behaved at random toward them. However focal lizards clearly recognised that their rivals were conspecifics given their propensity to escalate to an aggressive interaction. It is possible that other signals also aid individual recognition. For example, chemical recognition of rivals in lizards is well documented (Aragón et al. 2003), and behavioural signals such as head bobbing (Phillips 1995) are also used for indvidual recognition in some lizards. This study shows, however, that natural variation in gular colour pattern of the tawny dragon is itself sufficient for rival recognition to occur since upon obscuring it lizards did not behave predictably.

The gular colour patterns of tawny dragons are a potential cue for rival recognition since they develop before sexual maturity and remain stable throughout adulthood (Gibbons and Lillywhite 1981; Vannoni and McElligott 2009). There is unlikely to be a major cost associated with gular colour pattern since most predators of this lizard are avian and the gular is ventral (Stuart-Fox et al. 2003; McLean et al. 2010). The clear benefit of recognising rivals is for males to avoid the cost of repeated fights with rivals against which they have previously lost. Because gular colour pattern seems to be unique to each individual, further studies could assess its potential for use in individual recognition (Carazo et al. 2008).

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